

A comparative analysis of canyon and non-canyon populations of the deep-sea scavenging amphipod *Paralicella caperesca*

GRANT A. DUFFY^{1,2}, ZOE R.S. GUTTERIDGE¹, MICHAEL H. THURSTON¹ AND TAMMY HORTON¹

¹National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK, ²School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

Existing population studies of deep-sea amphipods have focused on species that inhabit deep-sea vent or trench environments but few cosmopolitan species have been studied. Here we provide new insight into the life history and population ecology of the pan-oceanic scavenging amphipod Paralicella caperesca and discuss the influence of nutrient-rich submarine canyon environments on the growth and reproduction of this species. Data were collected through the dissection and measurement of 2997 P. caperesca from 14 samples taken from abyssal plains, continental slopes and submarine canyons in the North-East Atlantic. Sexual dimorphism was less pronounced than observed for other scavenging amphipod species but females were significantly larger and had shorter antennae than males. The size of oostegites in female P. caperesca varied considerably within size classes, ovaries contained a relatively large number of oocytes, and no empty ovaries were observed. These factors, in combination with absence of mature females, suggest that P. caperesca practices semelparity, a reproductive strategy that complements the feeding strategy of this obligate necrophage. Five male and seven female size-grouped cohorts were identified for P. caperesca. Cohorts from deep-sea submarine canyon populations showed consistently larger mean total body lengths than non-canyon cohorts. Individuals from canyon samples also expressed sexual characteristics at smaller sizes than non-canyon individuals. We hypothesize that these trends are indicative of nutrient-mediated growth, maturation, and reproduction in P. caperesca. The species is able to grow and reproduce relatively quickly in response to increased nutrient input in canyon environments and therefore dominates scavenging amphipod assemblages.

Keywords: Amphipoda, abyssal, Atlantic Ocean, deep sea, necrophage, nutrient-mediated growth, semelparity

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INTRODUCTION

Scavenging amphipods are a vital component of the secondary production cycles that support numerous deep-sea ecosystems through organic carbon cycling and dispersal from large food falls (Stockton & DeLaca, 1982; Britton & Morton, 1994; Payne & Moore, 2006; Higgs *et al.*, 2014). However, knowledge of the population ecology and life histories of this group of necrophages is limited. Recent efforts in the study of these organisms have improved our understanding of their community level ecology (e.g. Thurston, 1990; Jamieson *et al.*, 2011; Duffy *et al.*, 2012; Horton *et al.*, 2013), but studies examining the factors that affect population structure and dynamics of deep-sea scavenging amphipods are underrepresented.

Population studies carried out on shallow-water amphipod species (see Sainte-Marie, 1991, for a review of pre-1990 literature; Arndt & Beuchel, 2005; Nygård *et al.*, 2009) provide a robust framework when examining and analysing deep-sea scavenger populations. However, deep-sea amphipod population studies have primarily targeted populations of deep-sea amphipod species from vent (Sheader *et al.*, 2000, 2004;

Sheader & Van Dover, 2007), canyon (Kaïm-Malka, 2003, 2004, 2005) and trench environments (Perrone *et al.*, 2002; Thurston *et al.*, 2002; Blankenship *et al.*, 2006; Eustace *et al.*, 2013). Cosmopolitan species have been studied to a limited extent with *Eurythenes gryllus* (Lichtenstein in Mandt, 1822) (Ingram & Hessler, 1987; Thurston *et al.*, 2002; Premke *et al.*, 2006; d'Udekem d'Acoz & Havermans, 2015) a notable example.

Paralicella caperesca Shulenberg & Barnard, 1976 has a pan-oceanic distribution in lower latitudes. It has been recorded from widespread localities in the Pacific Ocean (e.g. Shulenberg & Barnard, 1976; Yayanos, 1981; Ingram & Hessler, 1983; Hendrycks & Conlan, 2003; Jamieson *et al.*, 2011; Fujii *et al.*, 2013) within a depth range of 1720–6200 m (Wilson *et al.*, 1985; Hasegawa *et al.*, 1986), from the Indian Ocean (Treude *et al.*, 2002; Cousins *et al.*, 2013) and the Atlantic Ocean. The species has not been recorded in the Southern Ocean south of the Antarctic Polar Front (De Broyer *et al.*, 2004, 2007) or in the Arctic Ocean. There are many records from the North Atlantic (Barnard & Shulenberg, 1976; Thurston, 1979, 1990; Macdonald & Gilchrist, 1980, 1982; Smith & Baldwin, 1982; Lampitt *et al.*, 1983; Desbruyères *et al.*, 1985; Barnard & Karaman, 1991; Jones *et al.*, 1998; Bühring & Christiansen, 2001; Duffy *et al.*, 2012; Horton *et al.*, 2013), where it has been found in baited traps deployed at 2448 m on the Mid-Atlantic ridge (Horton *et al.*, 2013) down to 5940 m on the Iberian Abyssal Plain (Barnard & Shulenberg, 1976). Records

Corresponding author:

G.A. Duffy

Email: grant.duffy@monash.edu

from the Tropical and South Atlantic (Thurston, 1990; Hendrycks *et al.*, 2010) suggest that the species has a pan-Atlantic distribution. Virtually all of the *P. caperesca* specimens reported have come from baited traps set on, or within a few metres of, the sea floor but the species can occur well up in the water column. It has been taken in mid-water trawls more than 700 m above bottom in the Atlantic (Thurston, 1990) and more than 900 m above bottom in the Pacific (Ingram & Hessler, 1983). This broad geographic and bathymetric distribution is in spite of the limited dispersive ability, obligate brooding, and direct development that is characteristic of scavenging amphipods (Lincoln, 1979).

Very little is known of the life history of *P. caperesca* beyond inferences made from mouthpart and gut morphology. The mandibular molars are conico-laminate and non-triturative, and appear to act as a ratchet mechanism pulling strips of food cut by the broad incisor processes towards the oesophagus in a manner similar to that reported for *Alicella gigantea* Chevreux, 1899 (De Broyer & Thurston, 1987). The gut is capable of huge expansion, allowing the ingestion of large amounts of food implying the species is a highly specialized scavenger (Barnard & Shulenberg, 1976; Shulenberg & Barnard, 1976; Thurston, 1979). Thurston (1979) noted that sexual dimorphism of *P. caperesca* is limited to relative antenna length and that it is unlikely that females of this species are capable of producing multiple broods. Further study will provide vital information on the life history of this species and will lead to a better understanding of specialized scavengers in the deep sea.

Paralicella caperesca has been identified from many traps deployed on the abyssal plains of the North Atlantic, and has also been found in particularly high numbers within submarine canyons of the Iberian Peninsula, dominating traps deployed there (Duffy *et al.*, 2012). This allows for comparisons between populations of *P. caperesca* from submarine canyons and their counterparts from non-canyon environments. Submarine canyons form an interesting environment in which to study scavenging populations as they are often identified as hotspots of secondary production (Vetter, 1995; Soliman & Rowe, 2008; De Leo *et al.*, 2010; van Oevelen *et al.*, 2011), which may result in an increase in the number of food falls (Higgs *et al.*, 2014). This comparative study will allow a detailed examination of how the heightened secondary production of canyon environments is affecting growth and reproduction in scavenging amphipod species while elucidating life history traits of *P. caperesca*.

MATERIALS AND METHODS

Sample collection

Canyon populations of *Paralicella caperesca* were represented by specimens from seven samples, collected using baited traps, and sorted for community composition analyses (Duffy *et al.*, 2012; Table 1). All canyon samples were collected from submarine canyons off the western Iberian Peninsula as part of the HERMES project (Figure 1; Weaver & Gunn, 2009). Four samples were from baited trap deployments in Nazaré Canyon, two were from Setúbal Canyon, and one was from Cascais Canyon.

To allow comparison between populations in submarine canyons and those of non-canyon environments, commensurate samples were identified from the Discovery Collections (National Oceanography Centre, Southampton, UK). These

non-canyon samples were chosen on the basis that they contained sufficient numbers (>50) of *P. caperesca* and were collected at a similar depth, during the same year or at a similar time of year as the HERMES canyon samples (Table 1). Eight of these samples were from abyssal plains in the NE Atlantic (Figure 1; Porcupine, Madeira and Cape Verde Abyssal Plains), and one was from the Porcupine Seabight. The *P. caperesca* components of canyon and non-canyon samples were analysed as outlined below.

Data collection

For large samples (>600 *P. caperesca* individuals) all specimens were assigned a unique identifier number and a random number generator was used to select a random subsample of 200 individuals. Selected individuals were dissected and measured under a stereo-dissecting microscope. Specimens were preserved in a variety of postures and many were damaged, making it difficult to obtain total body length measurements for all individuals. Past studies have resolved this problem using a single body-part measurement as a proxy for total body length (Chapelle, 1995; Sheader *et al.*, 2000, 2004; Thurston *et al.*, 2002; Blankenship *et al.*, 2006; Sheader & Van Dover, 2007; Nygård *et al.*, 2009; Duffy *et al.*, 2013). In this study coxal plate 4 was used as a proxy for total body length.

The total body length (distance along the dorsal margin between the anterior margin of the head and the tip of the telson) of 50 intact, randomly selected, *P. caperesca* from sample D297/15734 was measured using a digital graphics tablet and HTML-assisted Measuring System (HaMS; Duffy *et al.*, 2013). These data were subsequently correlated to diagonal linear measures of coxal plate 4 (Figure 2; as in Chapelle, 1995), which were made using a stage graticule. Estimation of total body length for all remaining specimens was possible using the coxal plate 4 measurements as a proxy. Coxal plate 4 measurements, rather than estimated total body lengths, were used for population characterization analyses (see below) to reduce the effect of rounding errors that would be magnified through the scaling up of measurements.

Primary and secondary sexual characteristics permitted sexing of all but the smallest individuals, which were classified as unsexed juveniles. Together with coxal plate 4, antenna 1 (length, number of articles, accessory flagellum length), antenna 2 (length, number of articles), and secondary sexual characteristics (oostegite length and presence of oostegite setae in females, presence of genital papillae in males) were also measured. Oocytes within ovaries of females at varying stages of sexual maturity were measured and counted.

Population characterization

Characterization of amphipod populations relies upon the identification of discrete cohorts, or growth stages, representing successive moults. Each of these cohorts contains individuals of similar size but not necessarily similar age, owing to growth rate being affected by a range of environmental factors. Identification of cohorts is often possible by identifying normal distributions from polymodal length frequency distribution data of total body length or a correlated proxy (Sheader *et al.*, 2000, 2004; Thurston *et al.*, 2002; Kaïm-Malka, 2003, 2004, 2005; Blankenship *et al.*, 2006; Premke *et al.*, 2006; Sheader & Van Dover, 2007; Nygård *et al.*, 2009; Duffy *et al.*, 2013).

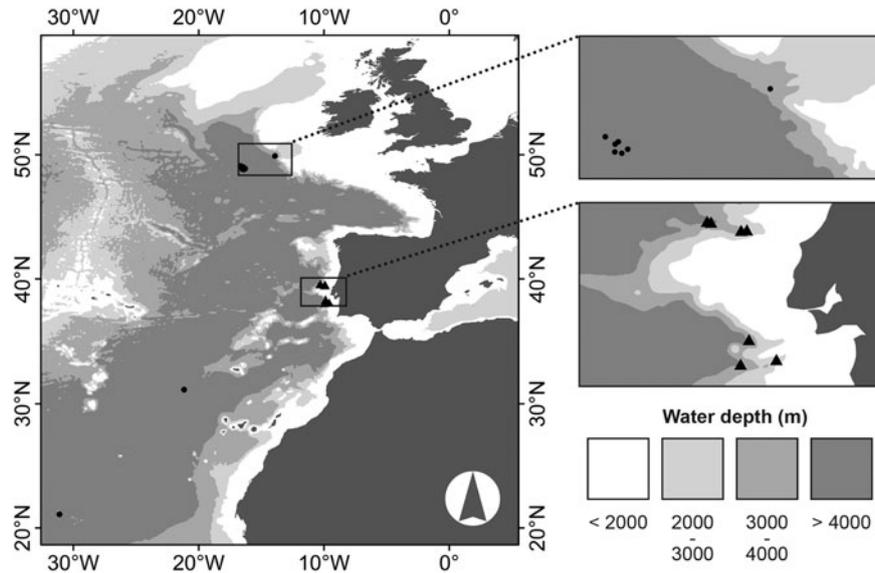


Fig. 1. Bathymetric chart of study areas coloured by water depth. Porcupine Abyssal Plain/Seabight and Iberian Margin shown in detail. Circles indicate non-canyon sampling sites and triangles indicate canyon sampling sites. See Table 1 for detailed sample collection information.

Oostegite measurements for females and coxal plate 4 measurements for males, females, and unsexed juveniles were plotted as probability density histograms. The identification of Gaussian components, each representing an oostegite stage or cohort, was performed initially by eye. The presence and parameters of each of these distributions were confirmed using the probability paper method (Cassie, 1954; Harding, 2009) and the 'mixdist' package (Macdonald & Pitcher, 1979; Macdonald & Du, 2011) in R statistical software (R Development Core Team, 2015). The goodness of fit of each of the modelled distributions was confirmed using the ANOVA function included in the 'mixdist' package.

Comparison of populations

Mann–Whitney *U* tests were used to compare distributions of male:female and juvenile:non-juvenile ratios between canyon and non-canyon samples. Once parameters for cohorts were

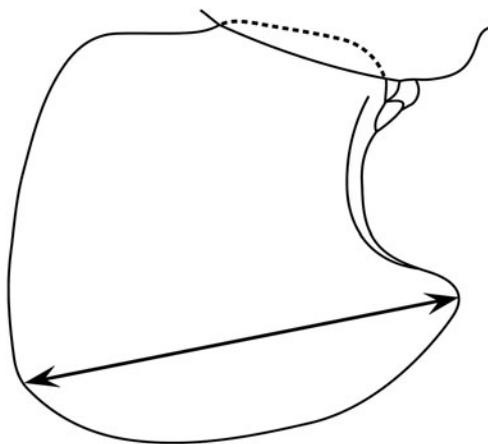


Fig. 2. Representation of coxal plate 4 of *Parallicella caperesca* (redrawn from Shulenberg & Barnard, 1976). Arrowed line indicates the diagonal linear measurement (as in Chapelle, 1995) used in this study as a proxy for total body length.

accurately determined, individuals from each sample were assigned to the appropriate cohort based on 95% confidence limits (2 SD from the mean). Where overlap of these limits occurred individuals were assigned to cohorts based on the relative proportions of each cohort. Following classification, population composition data were analysed using multivariate tests in PRIMER 6 (Plymouth Routines in Multivariate Ecological Research; Clarke & Gorley, 2006) statistical software. Data were root-transformed to reduce skewing and standardized to account for differing sample sizes. Following the creation of a Bray–Curtis similarity matrix, populations were compared using an ANOSIM test (Clarke, 1993) with sampling area (canyon, non-canyon) as the lone factor.

RESULTS

In total, 1422 *Parallicella caperesca* from canyon samples and 1575 individuals from non-canyon samples were dissected and measured. Males, females and juveniles were identified in all samples. No mature or ovigerous females were found. There was a positive correlation between coxal plate 4 length and total body length ($L = 6.8902C + 1.0610$, $R^2 = 0.6517$; where *L* is the estimated total body length and *C* is the linear measure of coxal plate 4, Figure 2). Although untransformed coxal plate 4 measurements were used for subsequent analyses, this relationship did permit the use of coxal plate 4 measurements as an indicative proxy to estimate total body length and allow for basic morphometric description and comparison of *P. caperesca* with other scavenging amphipod species.

Estimated total body length ranged from 1.70 to 22.34 mm. No individuals smaller than 4.65 mm showed primary or secondary sexual characteristics and were classed as juveniles. All individuals of 8.00 mm in length or more consistently exhibited primary and secondary sexual characteristics. A number of individuals smaller than 8.00 mm, mainly from canyon samples, could be sexed.

Table 1. Baited trap deployments for *Paralicella caperesca* used for this analysis. Shaded samples are from canyon sites using material from Duffy *et al.* (2012) with canyon name indicated in area column. Non-shaded samples are from non-canyon sites.

Station	Area	Location		Depth (m)	Date deployed (dd/mm/yy)	Bottom time (hh:mm)
		Latitude	Longitude			
CD179/56817	Setúbal	38.1528	-09.6000	3194	25/04/06	31:14
CD179/56855	Nazaré	39.5027	-09.9050	3499	11/05/06	23:02
D297/15734	Nazaré	39.4963	-09.9648	3600	01/08/05	21:28
CD179/56837	Cascais	38.3662	-09.8834	4230	02/05/06	30:17
D297/15741	Nazaré	39.5825	-10.2750	4286	04/08/05	24:22
CD179/56847	Nazaré	39.5917	-10.3167	4403	07/05/06	24:34
CD179/56839	Setúbal	38.1095	-09.9697	4445	04/05/06	24:12
D092/9756/008	PSB	49.8933	-13.9117	3852	13/04/79	04:15
D204/12600/044	CVP	21.0867	-31.1100	4540	09/10/93	10:45
Co85/52216/005	PAP	48.8337	-16.5070	4842	23/06/85	11:05
D229/13200/031	PAP	48.8132	-16.3905	4842	11/07/97	05:22
JCo71/034	PAP	48.9642	-16.5020	4846	05/05/12	40:00
JCo71/020	PAP	49.0048	-16.4497	4847	04/05/12	17:00
D194/12174/020	MAP	31.1267	-21.1667	4941	18/08/90	15:17

Area abbreviations: PSB, Porcupine Seabight; CVP, Cape Verde Abyssal Plain; PAP, Porcupine Abyssal Plain; MAP, Madeira Abyssal Plain.

Sexual dimorphism

Estimated total body length in males ranged from 4.65 to 18.97 mm (median = 10.12 mm, IQ range = 8.86–10.55 mm) and in females from 4.65 to 22.34 mm long (median = 10.97 mm, IQ range = 8.86–13.07 mm). There was a significant difference between the size distributions of males and females (Figure 3; Mann–Whitney U -test: $N = 963$, $U = 82,146$, $P < 0.001$). Males possessed significantly longer antenna 1 and antenna 2, relative to coxal plate 4 length, than females (MWU: $N = 948$, $U = 152,385$, $P < 0.001$; $N = 950$, $U = 171,933$, $P < 0.001$ respectively). The antennal differences between the sexes was most pronounced in antenna 2, with the antenna 1 to antenna 2 ratio significantly lower for males than females (MWU: $N = 940$, $U = 45,246$, $P < 0.001$) with males more commonly possessing second antennae of equal or greater length than their first antennae. As a function of antenna length (articles mm^{-1}) males possessed significantly more articles per mm of antenna length than females (MWU: antenna 1, $N = 753$, $U = 68,733$, $P = 0.015$; antenna 2, $N = 755$, $U = 84,405$, $P = 0.001$).

Sexual development

A pair of ovaries could be identified between pereonites 3 and 7, lying either side of the gut, in females as small as 4.65 mm. Complete ovaries were recoverable from 59 individuals. Both ovaries contained approximately equal numbers of spheroid oocytes of comparable size, densely packed in a three-tiered linear arrangement. Oocyte size, calculated as the area of an ellipse, showed a weak positive correlation with coxal plate 4 length, a proxy of total body length (Figure 4A). The total number of oocytes within each whole ovary ranged from 26 to 75, with a mean of 42.4 oocytes per ovary, but there was no apparent relationship between oocyte count and estimated body size (Figure 4B).

The smallest female with visible oostegite buds was an estimated 4.65 mm in length but most females of this size had no detectable oostegites and could only be identified by ovary presence. Larger females possessed oostegites of varying size.

A probability density histogram of oostegite length as a ratio of gill length (Figure 4C) identified four oostegite stages (OS₁–OS₄; Table 2) with minimal overlap. The presence and parameters of these stages were confirmed using the probability paper method.

No mature females with setose oostegites were found. Evidence of setal development was seen in some specimens possessing particularly large oostegites but in no case had setae evaginated. This suggests that these individuals were one moult away from sexual maturity. Testes were identifiable in the majority of males seen but were generally in poor condition making developmental classification impossible. Penile papillae in this species were small but could be identified on close examination of the underside of pereonite 7. The smallest male possessing visible penile papillae was an estimated 4.65 mm in body length.

Population characterization

Size distributions differed between the canyon samples and non-canyon samples, therefore separate cohort analyses were performed for each of these environments. Individuals that could not be sexed were assigned to four identified juvenile stages (Table 3, Figures 5 & 6). The parameters for the identified cohorts are comparable for the smallest individuals (J₁, J₂) but the separation between canyon and non-canyon cohorts becomes more pronounced at greater body length (J₃, J₄). Canyon cohorts have consistently larger mean total body lengths than their non-canyon counterparts.

A total of five male (Figure 5; M₃–M₈) and seven female (Figure 6; F₃–F₁₀) cohorts were identified (Table 3). The occurrence and parameters of these cohorts were confirmed using the probability paper method and a 'mixdist' model fitted to the data (ANOVA: Canyon males, d.f. = 19, $\chi^2 = 24.08$, $P = 0.1930$; canyon females, d.f. = 25, $\chi^2 = 51.88$, $P = 0.1243$; non-canyon males, d.f. = 19, $\chi^2 = 12.47$, $P = 0.8646$; non-canyon females, d.f. = 20, $\chi^2 = 25.53$, $P = 0.2634$). There was direct overlap between the largest juvenile (J₃, J₄) and smallest sexed (M₃, M₄, F₃, F₄) cohorts. Cohorts were numbered to reflect this.

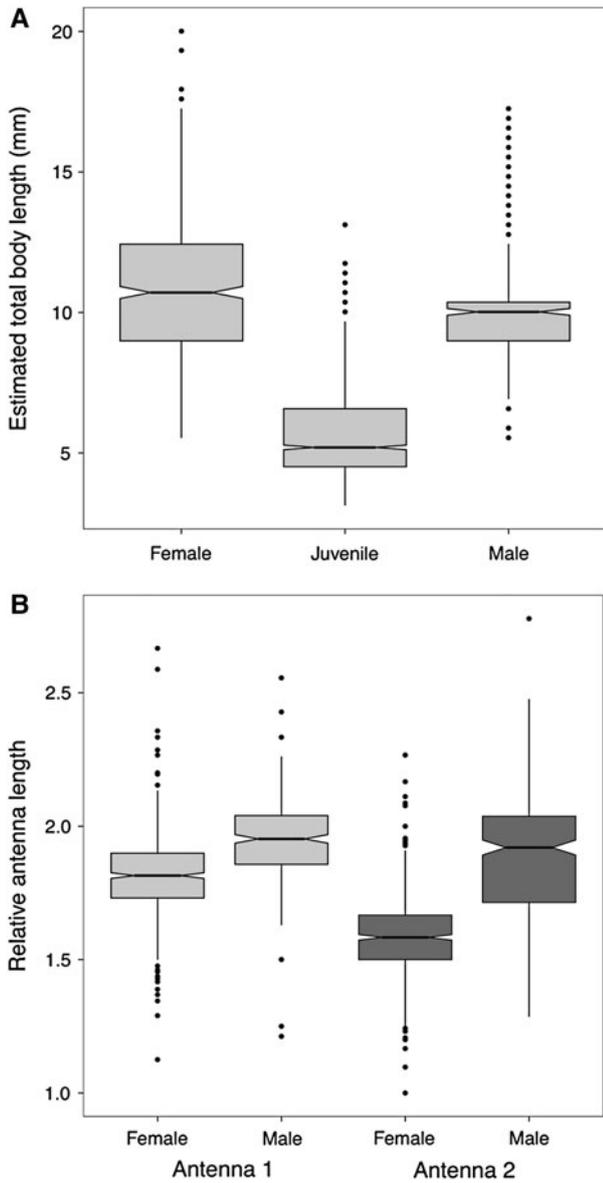


Fig. 3. Comparison between juvenile, male and female *Paralicella caperesca* from all sampling sites. Estimated total body length, using coxal plate 4 as a proxy, for males, juveniles, and females (A). Length of antennae as a function of coxal plate 4 length for antenna 1 and antenna 2 in male and female *P. caperesca* (B). Median and interquartile ranges shown, closed circles indicate individuals with estimated body length outside of the interquartile range.

Cohorts M3 and F3 were found almost exclusively in canyon samples with individuals of similar size from non-canyon environments rarely showing any sexual characteristics and therefore classified as J3 juveniles. The two cohorts containing the largest individuals (M8, F10) were not represented in canyon samples. Canyon cohorts showed consistently larger mean total body lengths than their non-canyon counterparts (Table 3; Figures 5 & 6).

Linear growth factors between cohorts were comparable to those reported for *A. abyssorum* (Stebbing, 1888) (Duffy *et al.*, 2013) and early stages of *E. gryllus* (Thurston, 1979; Ingram & Hessler, 1987). Increments between cohorts ranged from 1.10–1.44 with the largest growth increments between juvenile cohorts. Oostegite stages were distributed across female cohorts. More developed oostegites were more frequently

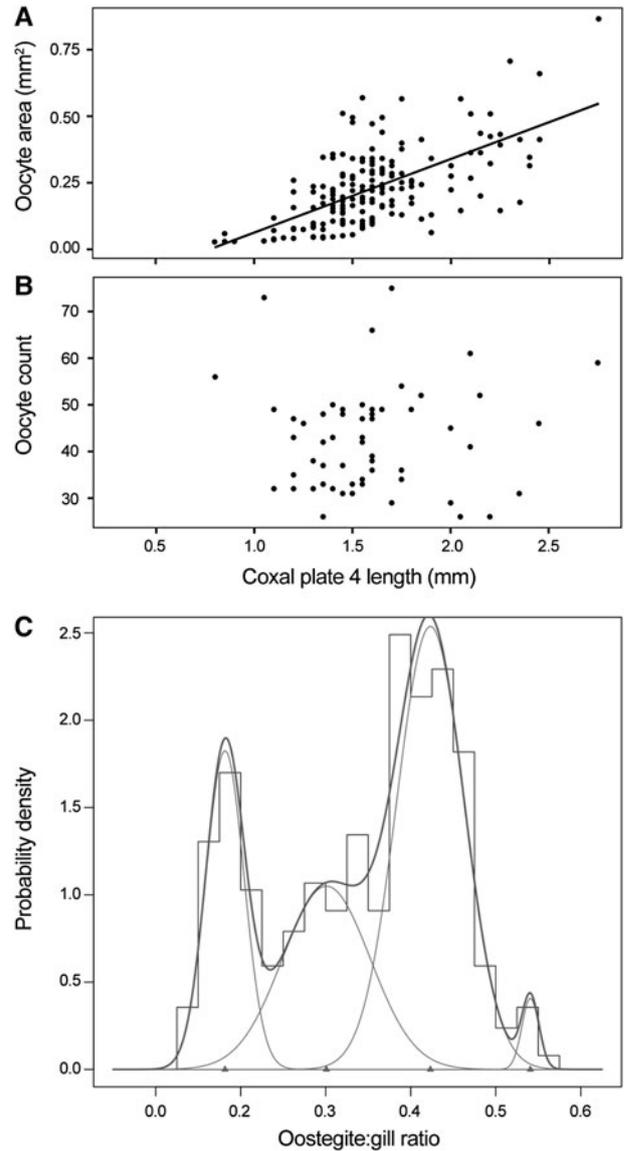


Fig. 4. Reproductive characteristics of female *Paralicella caperesca* individuals examined in this study. Oocyte size (A) and number of oocytes in each complete ovary (B) relative to the coxal plate 4 length, a proxy for body length, of each female where oocytes could be identified or complete ovaries were recovered. Oocyte size, calculated as the area of an ellipse, was weakly correlated to coxal plate 4 length ($R^2 = 0.3946$). Number of oocytes showed no correlation with coxal plate 4 length. Probability density histogram for oostegite:gill ratios for all female *P. caperesca* possessing oostegites from combined canyon and non-canyon samples (C). Normal distributions, identified using ‘mixdist’ package of R statistical software, indicated. Thin lines represent the distribution of each oostegite stage, thick line represents entire population.

observed in smaller individuals (F3–F6) from canyons than from non-canyon environments. The half-range of mature female body length (Sainte-Marie, 1991), a means proposed to distinguish between iteroparous and semelparous amphipod species, could not be calculated for *P. caperesca* as no mature females were available.

Population comparison

The male:female and juvenile:non-juvenile ratios did not differ significantly between canyon and non-canyon

Table 2. Counts of oostegite stage, identified by oostegite:gill ratios (OGR), for each female cohort of *Paralicella caperesca* from canyon and non-canyon sites.

	Oostegite stage	Mean OGR	F3	F4	F5	F6	F7	F8	F9	F10
Canyon	OS0	–	3	0	1	1	0	0	0	0
	OS1	0.16	26	14	14	0	0	0	0	0
	OS2	0.40	6	12	25	11	1	0	0	0
	OS3	0.64	1	4	76	112	4	1	1	0
Non-canyon	OS4	0.88	1	0	3	7	1	0	0	0
	OS0	–	2	0	0	0	0	0	0	0
	OS1	0.16	6	57	21	8	7	0	1	0
	OS2	0.40	2	18	30	29	9	2	2	0
	OS3	0.64	0	0	3	51	12	14	26	1
	OS4	0.88	0	0	0	2	3	1	0	0

environments (Table 4; Mann–Whitney *U*-test: $N = 14$, $U = 28.50$, $P = 0.620$; $N = 14$, $U = 27.50$, $P = 0.710$ respectively). Both ratios varied widely within test groups. Multivariate

analysis showed population composition based on cohort abundance varied significantly between canyon and non-canyon samples (ANOSIM: $R = 0.284$, $P = 0.020$).

DISCUSSION

Sexual dimorphism

Sexual dimorphism of *Paralicella caperesca*, while apparent, is less pronounced than in some other deep-sea scavenging amphipod species such as *A. abyssorum* (Duffy et al., 2013) and *E. gryllus* (Ingram & Hessler, 1987). Despite the lack of mature individuals, females were marginally larger than males in terms of estimated body length (Figure 3). This is in agreement with the pattern of inter-sexual size differences in lysianassoids demonstrated by Sainte-Marie (1991). *Paralicella caperesca* shares many characteristics with lysianassoids. As such, the observed size difference between males and females suggests that *P. caperesca* belongs to a group of species that practices non-mate-guarding pre-

Table 3. Mean coxal plate 4 measurement and estimated total body length (TBL) for all cohorts of *Paralicella caperesca* identified in this study from canyon and non-canyon sites. Linear growth factor between successive cohorts in parentheses.

	Juv. cohorts	C4 mean	TBL		Male cohorts	C4 mean	TBL		Female cohorts	C4 mean	TBL
Canyon	J1	0.40	3.79								
				(1.44)							
	J2	0.64	5.45								
				(1.27)							
	J3	0.85	6.90		M3	0.85	6.90		F3	0.86	6.95
				(1.22)				(1.22)			(1.26)
	J4	1.07	8.41		M4	1.07	8.41		F4	1.11	8.73
								(1.22)			(1.19)
					M5	1.33	10.25		F5	1.36	10.41
								(1.33)			(1.17)
				M6	1.83	13.64		F6	1.61	12.16	
							(1.09)			(1.24)	
				M7	2.00	14.84		F7	2.04	15.12	
										(1.18)	
				M8	–			F8	2.43	17.78	
										(1.08)	
								F9	2.63	19.16	
								F10	–		
Non-canyon	J1	0.44	4.07								
				(1.32)							
	J2	0.62	5.36								
				(1.20)							
	J3	0.78	6.43		M3	–			F3	–	
				(1.21)							
	J4	0.98	7.80		M4	1.07	8.44		F4	1.03	8.19
								(1.17)			(1.22)
					M5	1.28	9.90		F5	1.30	10.02
								(1.29)			(1.15)
				M6	1.70	12.77		F6	1.52	11.53	
							(1.12)			(1.20)	
				M7	1.91	14.24		F7	1.85	13.81	
							(1.12)			(1.08)	
				M8	2.15	15.90		F8	2.02	14.98	
										(1.12)	
								F9	2.27	16.72	
										(1.19)	
								F10	2.73	19.84	

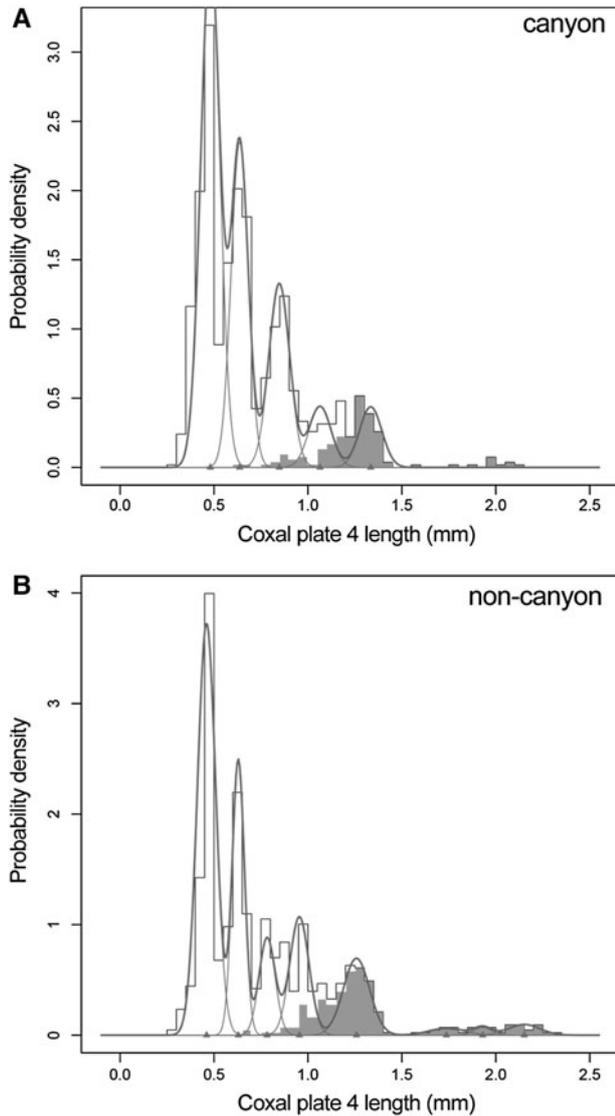


Fig. 5. Probability density histograms of coxal plate 4, a proxy for total body length, measures for all unsexed juvenile (unshaded) and male (shaded) *Paralicella caperesca* from canyon (A) and non-canyon (B) samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Thin lines represent distribution of each cohort, thick line represents entire population.

copulatory behaviour (Bousfield & Shih, 1994; Bousfield, 2001) as documented in lysianassoids by Conlan (1991). Males had significantly longer antennae with significantly more articles per mm of antenna length. The elongate antennae of male amphipods are believed to enhance chemosensing ability (Kaufmann, 1994) and tactile detection during mate searching (Steele, 1995).

Sexual development

No mature females were found amongst the 2997 specimens examined in the present study and Thurston (1979) identified only two mature females from a sample of 330 individuals taken at a depth of 4855 m in the North-East Atlantic. Ingram & Hessler (1983) did not indicate the proportion of adult female *P. caperesca* in their samples, so it is unclear as to whether the present observations represent the norm.

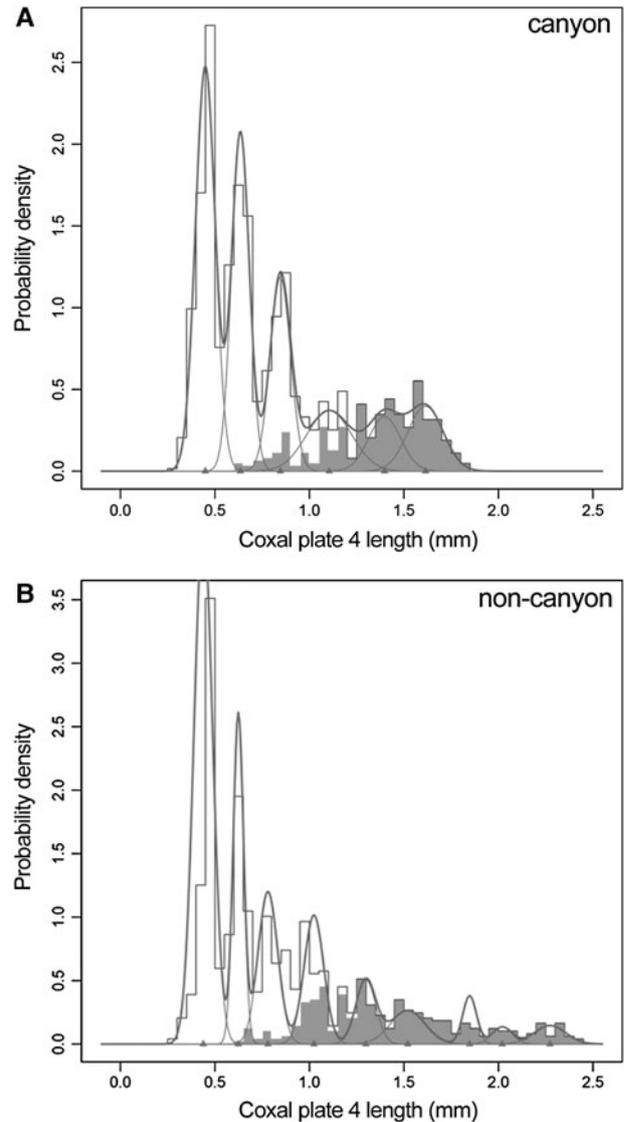


Fig. 6. Probability density histograms of coxal plate 4, a proxy for total body length, measures for all unsexed juvenile (unshaded) and female (shaded) *Paralicella caperesca* from canyon (A) and non-canyon (B) samples. Normal distributions, identified using 'mixdist' package of R statistical software, indicated. Thin lines represent distribution of each cohort, thick line represents entire population.

The near-absence of mature females in baited-traps suggests that *P. caperesca* is a semelparous organism as hypothesized by Thurston (1979).

The size of oostegites in female *P. caperesca* varied considerably within instars (Table 3), indicating a wide overlap of size ranges for succeeding developmental stages. This agrees with the pattern documented by Thurston (1979) in material trapped on the Horseshoe Abyssal Plain. A re-analysis of benthopelagic material from midwater hauls taken up to at least 720 m above the Cape Verde Abyssal Plain (Thurston, 1990) showed a similar pattern (juveniles 3–8 mm, juvenile females 6–12 mm, immature females 10–17 mm, adult females 9–11 mm) with the adult females taken at least 100 m above the sea floor. This common pattern indicates that sexual development is plastic in female *P. caperesca* and that maturity is likely reached in fewer instars in canyon populations than abyssal plain populations. In contrast,

Table 4. Total counts of males, females, and juveniles for all samples. Population composition ratios used for univariate comparison shown.

Station	Total males	Total females	Juv.	M:F ratio	Mature:Juv. Ratio
CD179/56817	22	13	28	1.69	1.25
CD179/56855	27	18	35	1.50	1.29
D297/15734	81	4	81	20.25	1.05
CD179/56837	80	33	400	2.42	0.28
D297/15741	8	12	180	0.67	0.11
CD179/56847	38	19	143	2.00	0.40
CD179/56839	80	33	400	2.42	0.28
D092/9756/008	71	46	35	1.54	3.34
D204/12600/044	21	14	127	1.50	0.28
Co85/52216/005	55	17	258	3.24	0.28
D229/13200/031	20	23	41	0.87	1.05
JCo71/034	46	64	88	0.72	1.25
JCo71/020	33	58	109	0.57	0.83
D194/12174/020	21	13	16	1.62	2.13

there is no size overlap between non-adult and adult males implying that development is fixed or at least less plastic than in females.

Based on the contents of all complete ovaries recovered, the maximum possible brood size of *P. caperesca* ranges from 52–150 offspring with a mean estimated brood size of 84. Contrary to the findings of Ingram & Hessler (1987) for *E. gryllus*, there is no apparent relationship between oocyte number and body length, in agreement with Thurston (1979), who observed that oocyte number in female *P. caperesca* was 'at most weakly related to body length'. Total oocyte counts were substantially higher than those reported by Duffy *et al.* (2013) for the bathyal scavenging amphipod *A. abyssorum*. Again using lysianassoid amphipods as a reference point, brood size loosely correlates with female body length but varies widely (Sainte-Marie, 1991). The estimated brood size of *P. caperesca* is substantially larger than that of most lysianassoids of similar size. The potential to produce large broods is in keeping with the hypothesis that *P. caperesca* is semelparous, investing substantial resources into one large reproductive event.

The frequency of the most developed oostegite stages (OS₃, OS₄) increased with increasing size-class number, however, no oostegites were setose regardless of oostegite stage and size-class. The lack of mature and ovigerous females leaves an important gap in our understanding of this species. As a result of the apparently semelparous lifestyle of *P. caperesca* it is unlikely that either of these development-classes will ever be caught using baited traps. The risks of predation at a food fall can be high (Lampitt *et al.*, 1983; Jones *et al.*, 1998; Janßen *et al.*, 2000; Jamieson *et al.*, 2009, 2011). Furthermore, the ability of *P. caperesca* to ingest huge quantities of food also results in a morphotype incompatible with brood retention (Shulenberger & Hessler, 1974; Shulenberger & Barnard, 1976; Thurston, 1979).

The hypothesis that *P. caperesca* is semelparous is further supported by the fact that no empty ovaries were identified in any females examined. A semelparous lifestyle has been

identified as a successful reproductive strategy for insects in environments with stable and predictable nutrient input (Fritz *et al.*, 1982, and references therein). If, as theorized, a semelparous strategy is practiced by *P. caperesca* this may go some way to explaining the dominance and apparent success of *Paralicella* species in submarine canyons (Duffy *et al.*, 2012), where nutrient input is elevated and relatively consistent.

Population characterization and comparison

The linear growth factors determined here for *P. caperesca* are comparable to those previously documented for this species (Thurston, 1979). These factors are lower than those of *A. abyssorum* (Duffy *et al.*, 2013) and early instars of *E. gryllus* (Thurston, 1979; Ingram & Hessler, 1987). They are similar to those reported for *O. gerulicorbis* (Thurston, 1979, as *Orchomene*), and higher than documented growth factors for *Scopelocheirus hopei* (Costa, 1851) (Kaïm-Malka, 2003) and *Tmetonyx similis* (Sars, 1891) (Kaïm-Malka, 2005).

There are marked differences in the population composition between the canyon samples and the non-canyon samples. The estimated mean total body length for each size-class was consistently higher for canyon size-classes than it was for their counterparts from the non-canyon environments. A number of environmental factors differentiating between these two sampling areas may be responsible for these differences. Canyon sites were generally shallower than non-canyon sites owing to their position on the continental slope. Therefore, canyon sites were also in marginally warmer water (Duffy *et al.*, 2012). While the non-canyon group included one shallower site not from the abyssal plain (D092/9756/008, 3852 m), this sample group was nevertheless skewed toward deeper sampling. Amphipod growth rates and adult body size increase at warmer temperatures (Sutcliffe *et al.*, 1981; Highsmith & Coyle, 1991; Pöckl, 1992; Panov & McQueen, 1998; Maranhão & Marques, 2003). However, the temperature difference between sample sites in canyons and non-canyon environments was very small (<0.1°C) compared with the temperature ranges used in laboratory experiments, making this explanation of the size differences between the populations unlikely.

Another possible explanation for the differing body-lengths between canyon and non-canyon populations is that the two environments support separate subspecies of *P. caperesca*. Despite the many records of this species from Pacific, Atlantic and Indian Oceans (see above), the only report of morphological variation is of minor differences between Pacific and Atlantic material (Barnard & Shulenberger, 1976). All of the material used in this study was obtained from a relatively circumscribed area in the North-East Atlantic Ocean lacking obvious physical barriers. This apparent homogeneity is in contrast with the significant morphological variation reported for *E. gryllus* (Thurston *et al.*, 2002; Stoddart & Lowry, 2004), shown subsequently to represent a species-complex containing at least five species (Havermans *et al.*, 2013; d'Udekem d'Acoz & Havermans, 2015). The *Eurythenes* species-complex shows a bathymetric as well as a geographic element in the genetic divergences separating the included entities (Bucklin *et al.*, 1987; Havermans *et al.*, 2013). All of the *P. caperesca* material used in this study came from depths exceeding 3000 m, a depth that appears critical for separating shallow and deep entities within the

Eurythenes complex (Havermans *et al.*, 2013). This suggests that bathymetry is not a prime cause of the differences observed.

Supported by the differences seen between populations of *A. abyssorum* in areas of different surface productivity (Duffy *et al.*, 2013), it appears that the most probable reason for larger total body length in canyon size-classes is a result of the increased nutrient input to canyon environments. While the availability of large food-falls to deep canyon sites is yet unknown, increased nutrient availability and heightened secondary production have been documented (Vetter, 1995; Soliman & Rowe, 2008; De Leo *et al.*, 2010; van Oevelen *et al.*, 2011). The high abundances of scavenging amphipods found in submarine canyons (Duffy *et al.*, 2012) lends further support to the theory that nutrient availability in an environment has significant effects on scavenging amphipods at both the community and population levels.

There are several possible explanations for the earlier onset of reproductive development in submarine canyon populations. As with growth rate, earlier reproductive development has also been attributed to temperature variations in other amphipod species (Sheader, 1983; Highsmith & Coyle, 1991), however, as previously discussed, water temperature in the sampled canyons was only marginally higher than at non-canyon sites (<0.1°C; Duffy *et al.*, 2012). Once again, the difference in nutrient availability between the two areas is an important consideration. A link between nutrient availability and sexual development in *P. caperesca* has been previously hypothesized by Thurston (1979). With an abundant food supply, individuals in canyons are able to apply resources to both growth and reproductive output allowing the onset of earlier reproductive development (Sutcliffe *et al.*, 1981). Earlier maturation and oostegite development with nutrient-rich conditions has been recorded in the scavenging amphipod *T. similis* (Kaïm-Malka, 2004). This developmental plasticity in response to food supply has also been observed in other amphipod species from very different habitats, such as the estuarine *Gammarus duebeni* Liljeborg, 1852 (Sheader, 1983) and the vent-dwelling *Bouvierella curtirama* Bellan-Santini & Thurston, 1996 (Sheader *et al.*, 2004). In the food-limited abyssal plains resources are more constrained and therefore input into reproductive development is delayed until further growth has been achieved.

Ecological implications

Paralicella caperesca has the characteristics of a semelparous organism capable of one reproductive event in a lifetime and, as demonstrated by its abundance and ubiquity (Thurston, 1979, 1990; Lampitt *et al.*, 1983; Barnard & Karaman, 1991; Jones *et al.*, 1998; Duffy *et al.*, 2012, 2013; Horton *et al.*, 2013), it is very successful in abyssal habitats. In his comparison of two scavenging fish species, *Coryphaenoides acrolepis* (Bean, 1884) and *C. armatus* (Hector, 1875), Drazen (2002) hypothesized that the latter, an abyssal species, is semelparous owing to the nutrient regime of the abyssal zone. While food supplies in the abyss are low, they are also generally stable. This means survivorship of both juveniles and adults is relatively constant, making semelparity a successful and energetically conservative reproductive strategy. The same appears to be true for *P. caperesca*.

The small, sexually mature, *P. caperesca* females identified in material reported by Thurston (1979, 1990) together with

variability in sexual development across size-classes reported in this study suggest that maturation, and hence reproduction, of *P. caperesca* relies on an environmental trigger rather than being purely age or size dependent. There is strong evidence that this trigger is primarily nutrient availability. As an obligate scavenger capable of gorging itself (Shulenberger & Barnard, 1976; Thurston, 1979), *P. caperesca* can capitalize on any high nutrient inputs into the abyss, such as large food falls, maturing and reproducing when these events occur. The expected increase in large food falls (Higgs *et al.*, 2014) driven by increased sediment input to the submarine canyon system and heightened productivity (Vetter, 1995; Soliman & Rowe, 2008; De Leo *et al.*, 2010; van Oevelen *et al.*, 2011) and the semelparity of *P. caperesca* allow this species to dominate canyon communities (Duffy *et al.*, 2012).

The semelparous lifestyle of *P. caperesca* provides an interesting contrast to *A. abyssorum*, another deep-sea scavenging amphipod that has been studied in comparative detail (Duffy *et al.*, 2013), which is more often associated with the bathyal zone (Horton *et al.*, 2013). *Abyssorhomene abyssorum* expresses the characteristics of an iteroparous organism capable of producing multiple broods of similar size to other iteroparous amphipod species (Sainte-Marie, 1991; Duffy *et al.*, 2013). It is a less specialized scavenger than *P. caperesca* and believed to be a facultative rather than obligate scavenger (Shulenberger & Barnard, 1976; Thurston, 1979). This may go some way toward explaining the differing reproductive strategies of these two species. Investing in a single, large, reproductive output in response to a food fall allows *P. caperesca* to maximize its success under the feast-famine regime experienced by obligate scavengers in abyssal environments and capitalize when the only nutrient resource it can consume becomes available. As *A. abyssorum* cannot gorge to the same extent as a specialist necrophage (Shulenberger & Barnard, 1976; Dahl, 1979; Thurston, 1979), a more generalist feeding strategy where smaller amounts are consumed at more regular intervals is likely. This strategy lends itself to the multiple smaller reproductive outputs of iteroparity. These differing reproductive and scavenging strategies have allowed these two species to become highly successful and abundant within their respective environments (Duffy *et al.*, 2012; Horton *et al.*, 2013).

Abyssorhomene abyssorum and *P. caperesca* have bathymetric distributions that overlap to a limited degree (Thurston, 1990; Horton *et al.*, 2013). Hydrostatic pressure and water temperature are often identified as factors controlling scavenging amphipod distributions and community composition (Thurston, 1990; Thurston *et al.*, 2002) but trophic conditions have also been implicated as a contributory factor (Premke *et al.*, 2006; Horton *et al.*, 2013). Our improved understanding of the contrasting feeding and reproductive strategies of scavenging amphipod species supports this theory. Obligate necrophages, such as *P. caperesca*, prevail in abyssal habitats, where background nutrients are poor and large inputs are likely to be patchy and often infrequent, through facultative breeding (i.e. based on food availability). If food and sufficient energy are available individuals will gorge, mature rapidly, breed, brood and die. Where episodic nutrient-rich inputs, such as large food falls, occur more frequently, species capable of earlier maturation and a large reproductive output when trophic conditions are favourable are able to dominate communities (Duffy *et al.*, 2012). In regions where the trophic conditions are more stable and

nutrients are less limited, generalists following an iteroparous lifestyle, with multiple small reproductive events, are at an advantage. *Abyssorhomene abyssorum* has adopted this lifestyle (Duffy et al., 2013) which may facilitate community dominance in shallower deep-sea habitats such as mid-ocean ridges (Horton et al., 2013). Deep-sea scavenging fishes of the genus *Coryphaenoides* show similar patterns in reproductive strategy differences between abyssal and bathyal habitats (Drazen, 2002).

This study presents strong evidence for semelparity and nutrient-mediated growth, maturation, and reproduction in *Paralicella caperesca*. Comparing canyon and non-canyon populations of this species highlights how this strategy affects population dynamics, with canyon cohorts having consistently larger body size and expressing sexual characteristics at a smaller size. These findings provide important insights into the ecology of deep-sea scavenging amphipods. Semelparity complements the obligate necrophagy practised by *P. caperesca* and has been pivotal to the success of this species in both abyssal and deep-sea submarine canyon habitats.

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Correspondence should be addressed to:

G.A. Duffy
School of Biological Sciences, Monash University, Clayton,
Victoria 3800, Australia
email: grant.duffy@monash.edu